

**Host Nest Discrimination by a Cleptoparasitic Fly,
Metopia campestris (Fallén)
(Diptera: Sarcophagidae: Miltogramminae)¹**

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ABSTRACT: Nine visual or olfactory cues potentially used in host nest selection were presented in artificial burrows to cleptoparasitic *Metopia campestris* females flying at an aggregation of nests of digger wasps, *Crabro cribrellifer*. These flies are visually attracted to holes in the ground, with subsequent discrimination among nests mediated by chemical cues probably derived from the host female.

Cleptoparasitic miltogrammine flies are formidable enemies of ground-nesting bees and wasps, and are commonly seen flying at nesting aggregations. Some species parasitize other insect groups (Orthoptera and Diptera) and may be useful for biological control of certain pest species (Thompson and Love, 1979). Despite their frequent abundance little is known as to how they locate their hosts. This subfamily (Diptera: Sarcophagidae: Miltogramminae) is often separated into two groups on the basis of larvipositing behavior (Ristich, 1953; Evans, 1970, for biology; Allen, 1926; Kurahashi, 1970, for taxonomy). "Satellite flies" (e.g., *Sentotainia trilineata*) pursue provisioning female wasps and larviposit on the prey while the host female is in flight, or as she is entering her nest. In this group the compound eyes of females have conspicuously enlarged anterior ommatidia (Allen, 1926), suggesting that cues used to locate hosts are primarily visual in nature. The second group consists of "hole searchers" (e.g., *Metopia campestris* of this study) which seek out nests, enter them, and deposit larvae; their ommatidia are not enlarged anteriorly (Allen, 1926). The study reported here evaluates responses of *M. campestris* to some visual and olfactory cues potentially used in the nest selection process.

Female flies possess a large pouch near the uterus in which ova develop into first instar larvae (=uterine larvae: Pantel, 1910; Townsend, 1911). Once in a cell of a host nest, larvae feed on the host's cached provisions. Typically the host larvae perish, although it is disputed whether the parasite larvae kill and eat host larvae or merely starve them by eating their provision (Pantel, 1910; Newcomer, 1930; Ristich, 1953; Evans, 1970; Endo, 1980).

Materials and Methods

Digger wasps, *Crabro cribrellifer* (Hymenoptera: Sphecidae), nesting in an aggregation at the University of Michigan Biological Station, Cheboygan Co., Michigan, were the predominant host species present (Wcislo, 1984; Wcislo et al., in press). Most parasite behavioral data were collected between 16 June and 12 August 1983, and experiments were performed between 14 July and 29 July 1984.

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Artificial nest burrows were constructed by driving in and withdrawing a nail (diameter = 7 mm, approximately the size of a *C. cribrellifer* nest entrance) 15 cm into the soil and forming a mound (=tumulus; height = 3 cm; diameter = 5 cm) around the entrance with appropriately colored soil collected at the site. Nine artificial "nests" were distributed in a 3 × 3 symmetrical grid (900 cm²) with each "nest" separated from its closest neighbor by 15 cm. This grid was randomly situated within the aggregation, with the condition that an active *C. cribrellifer* nest fell within its boundaries. During experiments this active nest was plugged and its mound removed. The same grid location was never used twice in the same day.

The following visual or olfactory cues were presented in or at artificial burrows to searching *Metopia* females: 1) Empty hole with normal mound. 2) Empty hole with large mound (height = 5 cm; diameter = 8 cm). 3) Empty hole with "Crabro" mound (these mounds were constructed with soil taken from active nests). 4) Empty hole with no mound. (One or two of the following cues were placed at the bottom of each artificial burrow). 5) *Typha* sp. (cat-tail) pollen. 6) Paralyzed robber fly (=prey used by *C. cribrellifer* females to provision their nests; Diptera: Asilidae). 7) Frozen *C. cribrellifer* female. 8) Cues (6) and (7) together. 9) Other frozen female wasp (*Ammophila* sp. or *Bembix* sp., Sphecidae).

For each test 4 cues were randomly drawn without replacement from this list, as were the 4 nail holes housing these cues. Each cue was either placed in a clean glass vial at the bottom of the 15 cm hole, or the mound was modified as required. A test lasted one hour, during which time the behaviors of flies approaching the test holes were observed and recorded as described below. This experimental design was modified in part from Cane (1983).

Attempts to individually mark female flies were futile (marked flies could not fly), and the following description of search behaviors is based on 98 observations of unmarked flies at the site in 1983. Female *Metopia* were commonly seen cruising about the aggregation at an altitude of 2–4 cm, following a characteristic flight pattern over a subsection (2 × 2–3 m) of the aggregation [Endo (1980) illustrates a similar pattern for *M. sauteri*]. The behavior of flies was recorded as follows:

APPROACH: A female flies or walks to within 2 cm of a hole.

PASS: A female approaches, and continues on its way.

CIRCLE: An approaching female rapidly circles a hole, flying at an altitude of less than 1 cm. Generally at least two circuits were made, with as many as 9 counted. The radius of the described circle was ca. 1 cm.

HOVER: After circling, a female sometimes hovers at the entrance, fanning the hole.

PERCH: After circling or hovering, a female frequently lands on the mound and sits at the rim of the hole, with the head typically oriented towards the entrance.

ENTER: A female walks into a nest, and remains inside for at least 2 seconds.

Transition frequencies between these behaviors are given in Table 1.

M. campestris females are most active when host females are most actively provisioning their nests (Wcislo et al., in press), and so testing was restricted to warm, sunny to partly cloudy days, between 1100 and 1600 hours (EDT). The number of female *Metopia* present over a 0.5 m² area, containing 8 active nests, was counted in a 5 minute period prior to the start of each experiment. These

Table 1. Transition matrix of frequencies of behaviors of *Metopia campestris* females approaching active nests of *Crabro cribrellifer* (from 1983, $n = 98$ observations). For each behavior (Behavior I) the frequency at which any other behavior immediately follows is given as Behavior II.

	Behavior II					
	Approach	Circle	Hover	Perch	Enter	Depart
Behavior I						
Approach	—	0.67	0	0	0	0.33
Circle	0	—	0.14	0.38	0	0.48
Hover	0	0	—	0.68	0.05	0.27
Perch	0	0	0	—	0.52	0.48

data are used as an index of parasite activity. This index remained approximately constant throughout the study ($\bar{x} = 3.5 \pm 0.07$ females/5 min), and so the data were not adjusted for parasite activity levels.

For all approaches the behaviors occurring immediately *before departure* were summed for each of the 9 cues and 6 behaviors (32 tests; 126 cue presentations). All biologically meaningful pairwise comparisons of the 9 cues for frequencies of PASS (unattractive) and ENTER (attractive) were analyzed using the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981). In order to maintain an experiment-wise error rate of $\alpha = 0.05$, each *a posteriori* pairwise comparison ($s = 36$, see Fig. 1) was considered significant at level $\alpha = 0.0014$, satisfying Bonferroni's inequality (Neter and Wasserman, 1974). Mean values are given with standard errors.

Results

The cumulative frequencies for each of the 5 behaviors (following APPROACH) occurring immediately before departure are given in Fig. 1 for each of the 9 cues tested. Flies passed empty artificial nests having mounds of various kinds (cues 1–4, Fig. 1) with similar frequencies. These data indicate that, at least initially, *M. campestris* females are visually attracted to holes in the ground. The addition of a mound does not make a hole more attractive to flies. Pairwise comparisons of the above cues (1–4) with "frozen *Crabro* female" (7) give significantly different frequencies of PASS for three comparisons (7 with 1, 2 and 4, $P < 0.0014$) and a nonsignificant difference for the fourth (7 with 3, $0.05 > P > 0.0014$). A greater attractiveness for holes containing a frozen female suggests that flies are discriminating between empty holes and host nests partly on the basis of chemical cues emanating from the host female.

Although "frozen *Crabro* female" (7) had the highest frequency of ENTER, for none of the pairwise comparisons were the differences significant at the conservative alpha level. In no cases were uterine larvae recovered from any of the test burrows, and it is unknown what cues are necessary to release larvipositing behavior.

Discussion

Studies of host selection by economically important insect parasitoids suggest that this process is appropriately viewed as a hierarchically structured series of "decisions" which serve to progressively reduce in size an area within which a

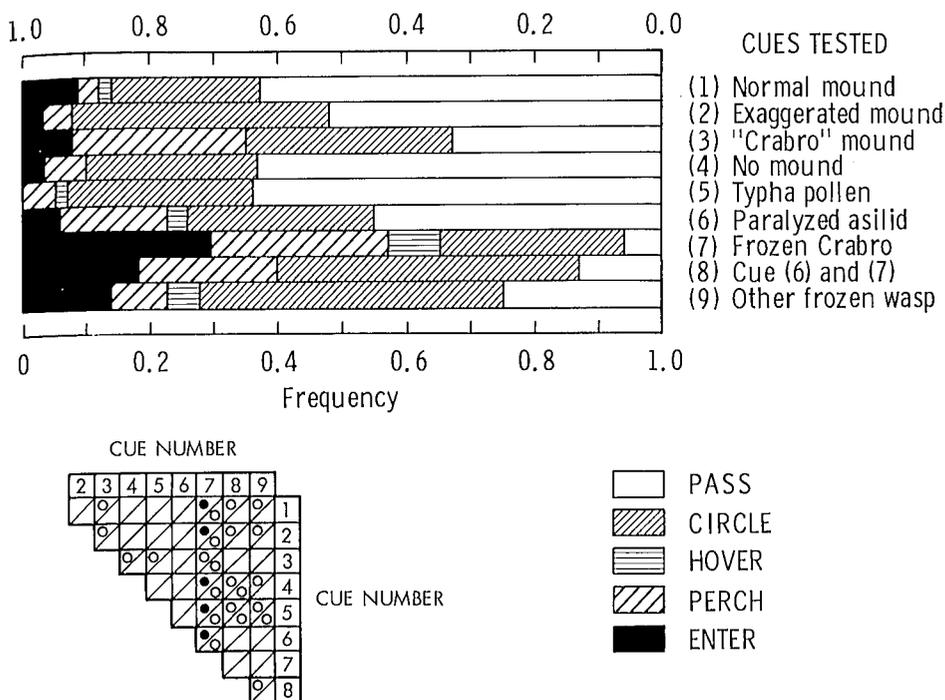


Fig. 1. Cumulative frequencies of *Metopia campestris* search behaviors in response to cues presented in artificial nests. The table at the lower left gives significance levels for all pairwise comparisons. Within each cell, the upper triangle represents frequency of PASS, and the lower triangle represents frequency of ENTER. Open circles: $0.5 > P > 0.0014$. Closed circles: $P < 0.0014$. Blank: $P > 0.05$.

parasitoid searches randomly (reviewed in Vinson, 1984). For most *M. campestris* locating a potential host population is probably passive, a consequence of philopatry to the natal aggregation, although no data are available on this point. Mating takes place at the aggregation (pers. obs.), lending some support to this conjecture.

Within a host nesting aggregation, orientation to potential nests is mediated by a combination of visual and olfactory cues. An empty hole with a mound was not more attractive than a simple hole in the ground. While conspicuous to observers, it is not surprising that mounds per se are not particularly attractive to flies. Nests of many wasps (Evans, 1966; Evans and West-Eberhard, 1970) and bees (Michener, 1974) have no mounds, as is obviously true for twig-nesting bees and wasps (Krombein, 1967), yet some of these are still parasitized by hole searching miltogrammines. "Crabro mounds" elicited fewer passes than "normal mounds," as well as a greater frequency of PERCH, indicative of greater attractiveness. These differences were not statistically significant, yet they do suggest some attractive chemical may adsorb onto the nest entrance substrate. Steinmann (1976) and Shinn (1967) postulate that such cues are used for nest recognition by various solitary bees, and Tsuneki (1968) suggests this for some pompilid wasps. Batra (1980) collected soil from mounds of *Colletes* (Colletidae) nests, and commented that this soil was attractive to female *M. campestris*.

Following the localization and recognition of a potential host nest, one might predict the fly will "assess" whether the nest is adequately provisioned to support her offspring. Concerning this question, the data presented above are inconclusive. Another miltogrammine, *Metopia sauteri*, frequently deposits larvae in its pompilid host nests before the cell is provisioned (Endo, 1980), as is apparently true for *M. leucocephala* parasitizing *Podalonia* (Sphecidae) (Newcomer, 1930), suggesting some species do not distinguish between provisioned and unprovisioned cells. Alternatively, females may simply distribute their larvae throughout the host population, adopting a "shot-gun" approach: larvae in suitably provisioned cells thrive while their less fortunate siblings in unsuitable cells perish. I do not know how long fly larvae are able to live without food. Two bits of data feebly support this alternative hypothesis. Females are rather fecund and can deposit many larvae (mean number of uterine larvae for 25 dissected females = 31.6 ± 3.11 , range = 7-61). Endo (1980) showed the mean number of *Metopia sauteri* larvae deposited in a single-celled nest of *Episyron arrogans* (Pompilidae) was 3.8 ± 2.8 ($n = 13$). Secondly, food items for developing larvae (5, 6) tested alone were not attractive, and the differences in attractiveness between "frozen *Crabro*" (7) and "*Crabro* and asilid" (8) were not significant. With respect to this latter comparison, the addition of this food item tended to decrease the overall attractiveness. Arguing against this "shot-gun" alternative is the fact that in no cases were uterine larvae recovered from test holes, which would be expected if flies were depositing larvae randomly into nests.

Differences in attractiveness among any of the cues testing a frozen wasp (7, 8, 9) were not significant; a particular species of wasp was not more attractive to the flies. This result is not surprising in view of the host-preference catholicism of many miltogrammines. In addition to attacking nests of *C. cribrellifer*, *M. campestris* has been observed parasitizing the following sphecids: *Crabro advena*, *Ammophila* sp., *Bembix* sp. (pers. obs.), *Chlorion ichneumoneum* (= *Sphex ichneumoneus*) (Ristich, 1953), and *Cerceris halone* (Byers, 1978). This species has also been observed at nesting aggregations of *Lasioglossum zephyrum* (Halictidae) (Batra, 1965; pers. obs.), and at an aggregation of three species of *Colletes* (Colletidae) (Batra, 1980), but as yet parasitization has not been documented in these bee nests. Similarly, Cane (1983) found no significant differences in the attractiveness of various host bees to searching parasitic *Nomada* bees. The low degree of host specificity of some cleptoparasites may be advantageous if a given host species is not always abundant, as seems likely.

It is simplistic to view the nest selection process as following a stepwise stimulus-response model. Taken as a whole, the available data suggest that at any level of assessment "attractiveness" is determined by an unknown weighting of both visual and olfactory cues. Visual cues are holes in the ground of an appropriate size, while the nature or source(s) of the chemical cues are unknown, although they are likely to be derived from the host females.

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